Breeding and feeding of two tit species in sympatric and allopatric populations

By

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Abstract. Breeding phenological parameters (density, clutch size, breeding success, nestling weight on day 15) and the food size distribution of the great tit *(Parus major)* and the blue tit *(P. caeruleus)* were studied in sympatric and allopatric populations, the latter one created by excluding one species from nest-boxes. An asymmetrical type of competition for food was found to be restricted to the parental care period. Blue tits fed their nestlings with larger caterpillars on the manipulated plot composed of blue tits only and with smaller ones when they bred sympatrically with great tits. Blue tits' specialisation on the smaller caterpillars does not present a disadvantage in the sympatric situation because these prey size categories are the most abundant ones in the supply. The utilization of differently sized prey items can be a possible cause of the differences in competitive abilities of the species during the parental care peroid.

Introduction

The great tit *(Parus major)* and the blue tit *(Parus caeruleus)* are the two most common breeding species in Central European deciduous forests. Competition and resource partitioning between the two species during different periods of the year was subject to a number of studies (reviewed by Alatalo, 1982). Several of these (Gibb, 1954; Betts, 1955; Dhondt & Eyckerman, 1980; Alatalo, 1981; Lister, 1981; Alatalo, 1982) showed that competition for food is important during winter. It has recently been suggested (Dhondt, 1977; Minot, 1981) that food can be a limiting factor during the breeding period, too.

This paper presents the results of a removal experiment where breeding phenological parameters and prey size distribution of the two tit species were compared in sympatric and allopatric situations. We hypothesized that if competition for food were important during breeding in allopatric populations (where the other species was prevented from breeding) the breeding phenological parameters would be better than in sympatric populations. This can result in higher breeding density, more eggs laid, larger nestling weights and

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higher fledging success of the allopatric population. If competition occurs during the whole breeding period (from the occupation of the territories to the fledging of the young), then we can expect a difference in all the parameters listed above. If, on the other hand, the competition is restricted to certain periods of the breeding season, then some of the above parameters would show a difference between sympatric/allopatric populations while others would not. If, for example, competition for food occurs during egg laying only, it will be reflected in clutch size; if competition is acting during the nestling period, the nestling weights will differ.

To prevent nesting site availability to become a limiting resource, we established a nest-box density of more than 10/hectare.

Study area and methods

The study was carried out in a mixed oak/hornbeam forest (Querco Petraeae-Carpinetum) near Budapest, Hungary. Two years before this study was started, most of the hornbeam trees were cut and the dead or fallen trunks were removed. Nest boxes were put out during the autumn 1981.

Three plots, 9 ha each, were established about 2 km from each other.

Plot 1: removal plot, allopatric for blue tit (BT). 100 nest-boxes were put out. The entrance hole diameter was 25 mm. Because of the small entrance diameter only BTs could breed on this plot.

Plot 2: control plot, sympatric populations of BT and great tit (GT). 200 nest-boxes were established. The entrance hole diameter was 32 mm. These nest-boxes could be utilized by the collared flycatcher *(Ficedula albicollis)* and the two tit species too. Some other species which occasionally bred here and on Plot 3 were marsh tit *(Parus palustris)*, nuthatch *(Sitta europaea)*, pied flycatcher *(F. hypoleuca)* and wryneck *(Jynx torquilla)*.

Plot 3: removal plot, allopatric for GT. 100 nest-boxes with an entrance diameter of 32 mm were put out. The entrance of boxes where we noticed a breeding attempt of the BT were closed. Breeding attempts of the BT were prevented this way throughout the whole breeding season.

Nest-boxes were checked every 3 – 4th day; clutch size, fledgling success (number of fledglings/number of eggs) and nestling weight (measured on the 15th day) were registered.

During the 1984 season, food samples using a modified neck-collar method (Török, 1981) were taken from nestlings on Plots 1 and 2. Low number of GT nests on Plot 3 prevented sampling for food on that plot. Nestlings from which food samples were taken were excluded from weight analysis.

Size distribution of the caterpillars on the trees was determined by measuring caterpillars collected by beating at the same time when food samples from nestlings were taken.

The niche width values were calculated using the Shannon formula (Shannon & Weaver, 1949).

Results

Breeding parameters

The breeding density of the two tit species varied between 0.8 and 1.8 pair/ha in different years and plots. The difference between the mean clutch size in the control and the removal plots was not statistically significant (Table 1), nor fledging success differed significantly for either species in any of the plots. We note, however, that all nests were included in the fledging success calculations including those which failed to hatch. Especially in 1984, the fledging success of both species was very low due to the heavy rainfall which caused a low hatching rate.

Table 1. Breeding density, clutch size and fledging success of the two species

Year	Species	Plot	Density (pair/ha)	Mean clutch size	Fledging success
1982	Blue tit	control	1.2	12,1	.74
		removal	1.2	12.1	.88
	Great tit	control	1.0	9.6	.76
		removal	1.1	10.3	.70
1983	Blue tit	control	1.0	12.8	.91
		removal	0.8	12.4	.91
	Great tit	control	1.6	11.4	.69
		removal	0.8	10.9	.50
1984	Blue tit	control	0.8	11,7	.56
		removal	1.3	12.5	.74
	Great tit	control	0.8	10.7	.47
		removal	0.9	10.5	.38

Nestling weights

Nestling weights, measured on the 15th day, did not differ significantly between the control and the removal plots in 1982 (Table 2). In 1983 and 1984, however, BT youngs were heavier in nest-boxes on plot 2 than on plot 1. This difference was slight in 1983 ($t = 2.45$, $p = 0.02$, two tailed test) and higher

Table 2. Nestling weight of the great tit and the blue tit at 15 days of age (g). (n is the number of nestling)

Year	Species	Control plot			Removal plot			Student's t-test two-tailed
		$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	
1982	Great tit	18.3	1.03	107	18.4	1.13	60	ns
	Blue tit	12.0	0.81	103	11.9	0.69	105	ns
1983	Great tit	16.6	1.81	100	18.1	1.81	26	$p = 0.001$
	Blue tit	11.8	0.79	104	11.5	0.74	79	$p = 0.02$
1984	Great tit	16.3	1.48	38	17,4	1.26	40	$p = 0.002$
	Blue tit	12.0	0.73	43	11.5	0.89	83	$p = 0.001$

in 1984 ($t = 3.39$, $p = 0.001$). The opposite trend was found for the youngs of the GT: they were heavier on plot 3 (BT removed) than on the control (plot 2). This difference was statistically highly significant (1983: $t = 3.61$, $p = 0.001$; 1984: $t = 3.42$, $p = 0.002$).

Food of the nestlings

Caterpillars dominated in the food of the nestlings of both species (Table 3). BT parents fed their young with more spiders and lepidopterous pupae and fewer small-sized tortricid caterpillars on plot 1 than on plot 2. GT parents brought more large-sized noctuid larvae than the BT parents did. The size analysis of the most important prey group, the lepidopterous larvae, showed that BT nestlings were fed with larger caterpillars on plot 1 (where GT was excluded) than on plot 2 (where both species bred, see Table 4). GT prefered the larger caterpillars on the latter plot. Mean prey size of the BT was 2.1 mm larger than the mean size of the caterpillars in the supply on plot 1. This difference was only 0.8 mm on the control plot (plot 2). The prey size niche width of the BT was larger (3.91) on the plot 1 where GT was excluded than on plot 2 where it bred with the GT (3.66).

Table 3. The food composition of the two tit species in 1984

Taxa	Great tit control plot	Blue tit	
		removal plot	control plot
Isopoda	–	–	1
Coleoptera			
Melolonthidae	1	–	–
Coleoptera larvae	–	–	2
Lepidoptera larvae			
Tortricidae			
Tortrix viridana	1	3	24
Tortricidae indet.	–	9	6
Lymantriidae	2	–	–
Geometridae			
Colotois pennaria	1	15	1
Operophtera brumata	7	3	16
Erannis spp.	24	33	38
Geometridae indet.	10	15	36
Noctuidae			
Orthosia stabilis	25	–	15
Orthosia cruda	24	1	–
Agrochola sp.	–	–	1
Noctuidae indet.	6	6	9
Lycenidae	1	1	–
Lepidoptera indet.	–	–	1
Lepidoptera pupae	2	33	2
Diptera			
Muscidae	–	–	3
Araneidea			
Thomisidae	1	43	17
Argiopidae	–	8	2
Lycosidae	1	–	–
Salticidae	–	7	1
Araneidea indet.	–	10	1
Total	106	187	176

Table 4. The mean size of caterpillars (mm) in the supply and in the food of the two tit species on the control and removal plots in 1984. (n is the number of caterpillars)

	Control plot			Removal plot			F-test
	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	
In the supply	15,0	4.01	521	16.2	6.09	252	p = 0.001
In the food							
blue tit	15.8	3.24	146	18.3	4.40	87	p = 0.001
great tit	19.9	4.68	101	–	–	–	–

Discussion

Recent studies have shown that the two common tit species, the GT and the BT, can compete in certain periods of the year. Competition during winter is well documented (Gibb, 1954; Betts, 1955; Alatalo, 1981; Lister, 1981; Alatalo, 1982): food is in short supply and roosting hole availability is also limited (Dhondt & Eyckerman, 1980). Early in the spring there is intraspecific competition for territories in areas of high population density in both the GT (Krebs, 1971) and the BT (Dhondt et al., 1982).

Opinions are different on the importance of competition during the breeding season. Research workers in England (Hartley, 1953; Gibb, 1954; Betts, 1955; Edington & Edington, 1972) argue that food is superabundant during this period and therefore this resource is not competed for. On the other hand, studies of the breeding success (Dohndt, 1977; Minot, 1981) and the food of the nestlings (Minot, 1981) showed that food can be a limiting factor during the breeding period, too.

Our results suggest that there is no competition for food during the period of egg laying because the breeding parameter characterizing this, the clutch size, did not differ among the control and the removal plots in either of the species. Food supply increases gradually during the incubation period and as the nestlings are not yet hatched, the consumption does not increase so competition is not probable during this period, either. During brood raising, however, the amount of the food can become a limiting factor which is reflected in the differences found in the weights of the nestlings on different plots. An asymmetric effect was found: GT youngs were smaller in broods on plots where BT also bred than on plots where BT was excluded from. This trend was not found in the BT nestling weights. Nestling weights do not allow an exact interpretation of the effect of GT on BT, but the study of the food of the nestlings showed that BT parents brought smaller caterpillars when breeding together with the GT and larger ones when breeding alone. The prey size niche width of the BT also decreased when it was sympatric with the GT. This shift, however, means no disadvantage for the BT because the direction of the shift along the prey size spectrum brings it to the size of the most abundant prey items. The abundance of the smaller caterpillars (14 – 18 mm) is so high that their biomass (dry mass × abundance) exceeds that of the large ones (18 – 22 mm). Collecting larger caterpillars is a less efficient way of feeding the young as it was reflected in the smaller fledgling weight of the GT youngs on the plot where it bred with the BT. Unfor-

tunately, the effect of BT on GT prey size preference was not possible to evaluate (see Methods). The utilization of differently sized prey items can be a possible cause of the differences in competitive abilities of the two species.

Although food is an important factor in the outcome of the competition between the two species, further studies are needed to clarify the role other factors like intraspecific competition, predation risk, the abundance and feeding of another potential competitor, the collared flycatcher play in the interspecific competition of the two tit species. This latter can especially be important as the collared flycatcher is one of the most abundant hole-nesting species in Central European forests whose breeding phenology and food is similar to the tits'.

Our data seem to support DHONDT'S (1977) suggestion that the two tit species are in asymmetric competition and the BT is superior. However, our data suggest that this competition is restricted to the parental care period only.

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